## *The hippocampus and spatial representation*

**AIMS**

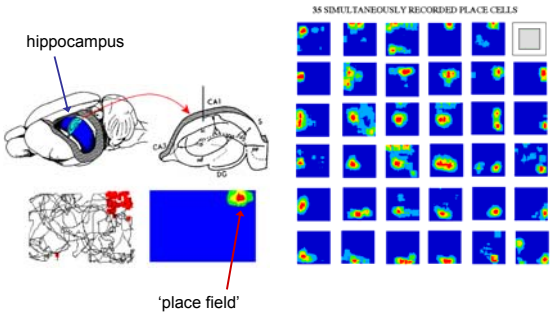
• Explain how unsupervised competitive learning could lead to the formation of location-specific firing in hippocampal 'place cells', and how the rat's movement during learning would determine the effect the rat's orientation has on their firing rates (Sharp, 1991).

• Discuss Sharp's model & subsequent expts. Inputs sensitive to the distance of landmarks appear to be present (O'Keefe & Burgess, 1996), but place cell firing is probably non-directional to start with (not learned) & a fixed feed-forward model is sufficient to model the firing of cells (Hartley et al., 2000; Zipser, 1986). Synaptic plasticity may be required, but for stability and robustness of place cell representation (Kentros et al., 2000; Nakazawa wt al., 2002).

**READING**

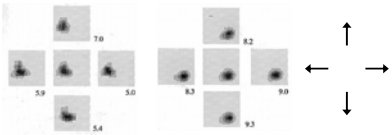
- Book 13.
- Zipser in Book 2.
- Sharp P E (1991) `Computer simulation of hippocampal place cells', *Psychobiology* 19 103-115.
- Hartley T., Burgess N., Lever C., Cacucci F., O'Keefe J. (2000) Modeling place fields in terms of the cortical inputs to the hippocampus, *Hippocampus* 10 369-379.

## 'Place cells' encode the rat's current location

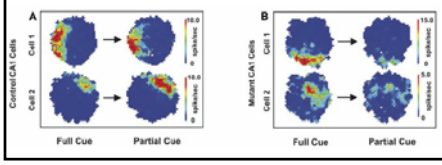



## Some properties of place cell firing.

• Does not depend on the rat's orientation in an open-field, but does on narrow-armed mazes.



• Is robust to the removal of subsets of cues (CA3 NMDA dependent), but strongly affected by interchanging cues.

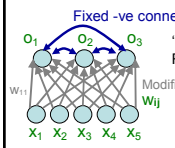



Nakazawa et al., (2002) Requirement for Hippocampal CA3 NMDA Receptors in Associative Memory Recall. *Science* **297** 211-218.

Recap: Unsupervised learning, example 1:

## Competitive learning

Fixed -ve connection weights



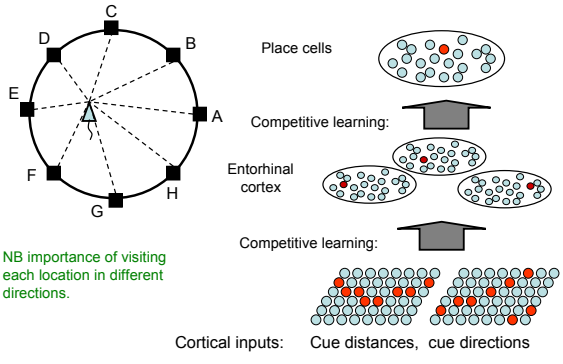

'Lateral inhibition' => one 'winner' if strongly activated enough Rumelhart and Zipser (1986). 'Winner-takes-all' architecture.

Threshold linear units.

- Random initial connection weights
- Present input pattern $\underline{x}^n$
- winner: output $o_k$ (i.e. $h_k > h_i$ for all $i \neq k$) set $o_k=1$, $o_i=0$ for all $i \neq k$
- Hebbian learning: $w_{ij} \rightarrow w_{ij} + \varepsilon\, o_i\, x_j^n$ i.e. $w_{kj} \rightarrow w_{kj} + \varepsilon x_j^n$, other weights don't change.
- Normalisation: reduce total size of connection weights to each output (so $|\underline{w}_i| = 1$) by dividing each by $|\underline{w}_i|$ or using alternative combined learning rule: $w_{kj} \rightarrow w_{kj} + \varepsilon(x_j^n - w_{kj})$
- Present next input pattern..

The output whose weights are <u>most similar</u> to $\underline{x}^n$ wins and its weights then become <u>more similar</u>. Different outputs find their own clusters in input data.

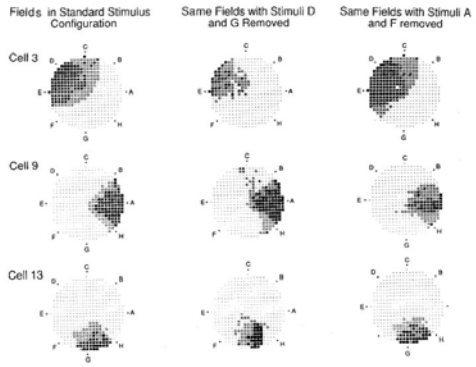
## Sharp's (1991) model of place cell firing




NB importance of visiting each location in different directions.

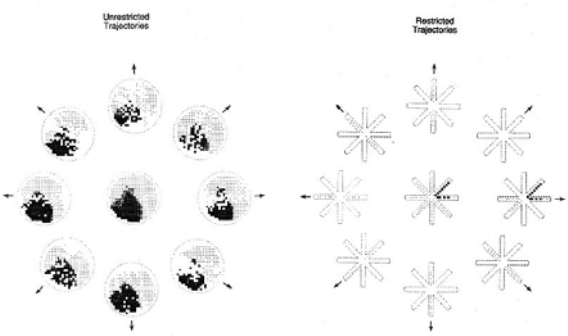
## Sharp's model cont.,

Simulated place cell firing is resistant to cue-removal.



## Sharp's model cont.,

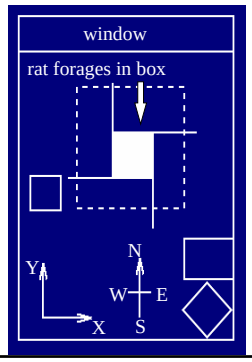
After random exploration, simulated place cells learn to show omni-directional firing, but not after directed exploration

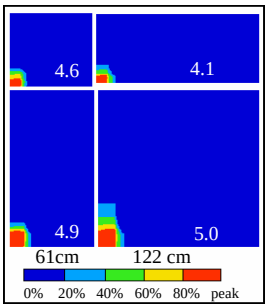



## What are the inputs to place cells?

Place fields in a deformable box

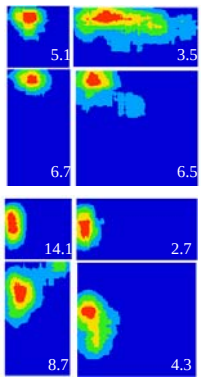
*O'Keefe & Burgess, 1996*



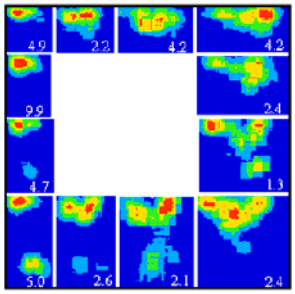




- simple place field in 4 rectangles

## 'Stretchy' place fields



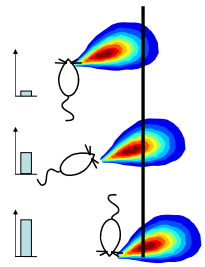

Place fields appear to respond at fixed distances from walls, with nearer walls more important than further ones.




## Functional model of place cell inputs

Firing Rate

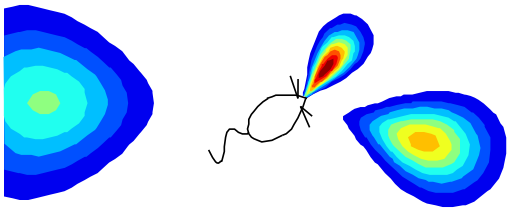
Receptive Field



Boundary Vector Cell (BVC)

- Each BVC tuned to respond when a barrier lies at a specific distance from the rat in a particular *allocentric* direction.

*Hartley et al 2000*

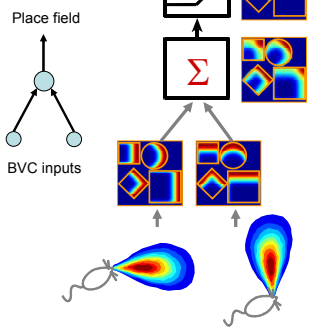


- Sharper tuning for shorter distances: each BVC input $g_i$ responding maximally at radius $d_i$ and bearing $\phi_i$ is described by:

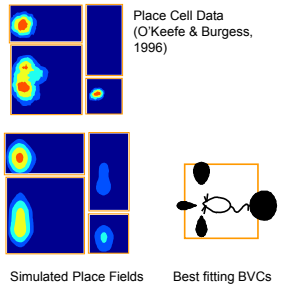
$$g_i(r,\theta) \propto \frac{\exp[-(r-d_i)^2/2\sigma_{rad}^2(d_i)]}{\sqrt{2\pi\sigma_{rad}^2(d_i)}} \times \frac{\exp[-(\theta-\phi_i)^2/2\sigma_{ang}^2]}{\sqrt{2\pi\sigma_{ang}^2}}$$

## Simulating place fields

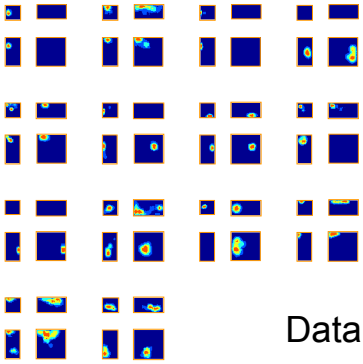
- BVCs have firing fields that follow the walls of the environment.
- Place fields are modelled as the thresholded sum of 2 or more BVC firing fields.



## Modelling a place cell with BVCs

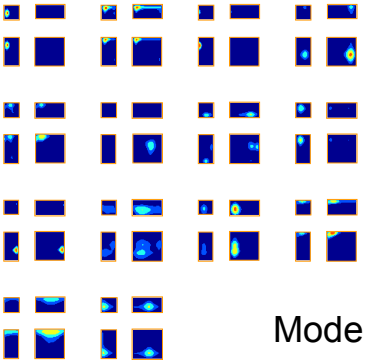



- 2-4 BVCs orientated at right angles to one another + threshold are sufficient to fit most fields.



Data

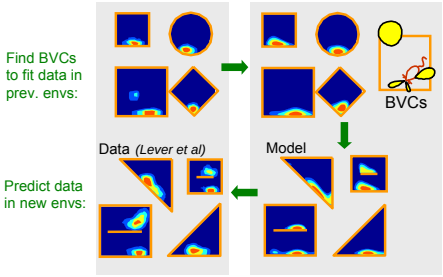
*O'Keefe & Burgess (1996)*



Model

*Hartley, Burgess, Lever, Cacucci, O'Keefe (2000)*

Place cell firing in new environmental layouts can be predicted using BVCs.




BVCs subsequently found in subiculum (& entorhinal cortex?)

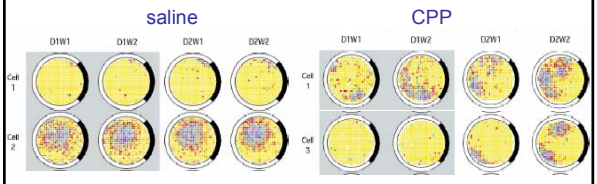
strong *remapping* of simult. recorded CA1 place cells

*Lever, Burton, Jeewajee, O'Keefe, Burgess, J Neurosci 2009*
*see also Barry et al., 2006; Solstad et al., 2008; Savelli et al., 2008.*

## Is synaptic modification required to to explain place cell firing?

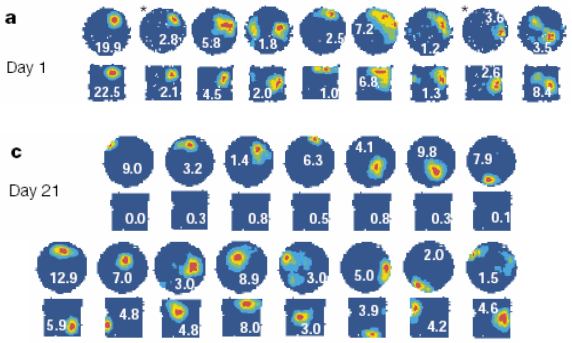
Yes:

1. Place field stability in a novel environment depends on NMDA receptors (Kentros et al., 2000), and robustness to cue-removal (Nakazawa et al., 2002).

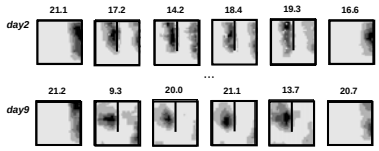



Abolition of Long-Term Stability of New Hippocampal Place Cell Maps by NMDA Receptor Blockade C Kentros, E Hargreaves, R D. Hawkins, E R. Kandel, M Shapiro, R U. Muller. (1998) Science 280: 2121-2126.

2. Slow experience-dependent ‘remapping’ of the place cell representation (Lever et al., 2002)




3 .Place cells do distinguish locations *with experience*

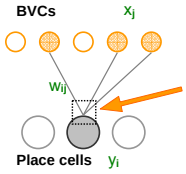



*Barry et al., (2006)*
*Rivard et al. (2004)*

# Summary

- Sharp’s competitive learning model explains robustness and directionality of place fields.
- Learning is not required for place cell firing *per se* (and not for omni-directional firing): simple feed-forward model suffices (Hartley et al., 2000), given the right type of input (“boundary vector cells”).
- Learning is required for place field robustness and stability over time (and in CA3 – see Lecture on ‘Hippocampus as an associative memory’)

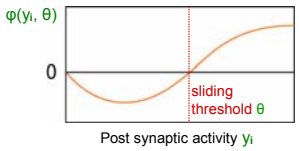
## Extended BVC model: adding learning




- **Update weights using BCM rule**

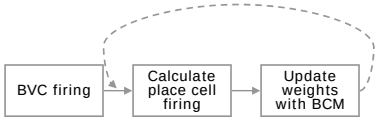
  requires pre & post-synaptic activity ($x_j$ and $y_i$)
  reduction if post-synaptic activity low
  increase if activity high

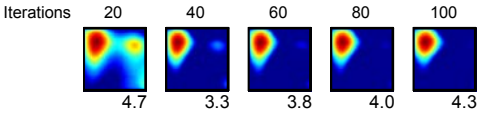
$y_i = f(\sum_j w_{ij} x_j)$
$\Delta w_{ij} = x_j \varphi(y_i, \theta)$
$\theta \sim \langle y_i^2 \rangle$




*Barry & Burgess (2007)*

## BVC model with learning




## Simulations